

Do coloured-winged damselflies and dragonflies have flight kinematics different from those with clear wings?

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The flights of male odonates encountering conspecifics at their reproduction sites were investigated by means of slow-motion films. We recorded large and generally consistent differences between species with clear wings (SCLW) and species with coloured wings (SCOW). SCLW mostly fought having physical contact and moved their wings without pauses in wing beats (hereafter designated wing pauses), attacking the other males. During encounters, SCOW males showed pauses of all wings or of the fore or the hind wings only. The wing beat frequencies of SCOW therefore showed much greater variation than in SCLW. In Zygoptera SCOW, parallel flapping of both wing pairs was frequent. The two investigated species of Calopterygidae showed several special flight patterns when encountering other males. Male Anisoptera with coloured wings also used wing pauses, and often displayed their wing patterns by gliding and banking to the other male or by flying in an upright posture. Thus, we found that most odonate males with coloured wings, in the presence of rivals, exhibited special flight styles, implying signalling functions. We interpret wing pauses as an adaptive characteristic that allows rival males to evaluate the quality of their opponent by assessment of the coloured wings. Sexual selection is suggested as a possible cause for the evolution of these flights.

Keywords: dragonfly flight; coloured wings; kinematics; wing beat frequencies; flight velocities; signalling; sexual selection

Introduction

Until now, the kinematics of odonate flight have been analysed mainly to study its aerodynamics (Usherwood & Lehmann, 2008; Wakeling & Ellington, 1997; Wang, 2008; Wang & Russell, 2007). Patterns of wing movement during flight differ in general between the suborders Anisoptera and Zygoptera in ways that are clearly correlated with their different morphological features. Within each suborder, however, differences among the flight kinematics of the species are more subtle, owing to similar morphology of bodies and wings (Rüppell, 1989). Based on phylogenetic analyses that included both recent and fossil taxa (Bybee et al., 2008; Davis et al., 2011), it seems plausible that the thorax and wing morphology of Epiophlebiidae and Lestidae approximate the ancestral condition within Anisoptera and Zygoptera, respectively. Our previous studies of *Epiophlebia superstes* and *Lestes viridis* exemplify these groups. Both have clear wings and show very uniform flight, i.e. mostly a counterstroking mode in which the fore and hind wings always move in opposite directions (Rüppell, 1989; Rüppell & Hilfert, 1993; Rüppell & Hilfert-Rüppell, 2009b).

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Counterstroking has also been described for special manoeuvres such as hovering in Anisoptera. The benefit of counterstroking is that it reduces body oscillations and saves aerodynamic power (Wang, 2008). But in Anisoptera the main wing beat pattern is phase shifting of the fore and hind wings, so that one pair of wings follows the other with a delay of about 1/4 period. These interactions between fore and hind wings increase the power output (Usherwood & Lehmann, 2008). Parallel beating, in which both pairs of wings beat nearly simultaneously in the same direction, occurs in all Odonata for a few wing beats in special manoeuvres such as backward or upward flight. Males of Zygoptera with coloured wings, such as *Calopteryx splendens* and *Megaloprepus caerulatus*, fly most of the time using this conspicuous parallel wing beating (Rüppell, 1985, 1989). The benefit is a greater net force, usable for acceleration; the cost is greater power expenditure (Wang & Russel, 2007). Assuming that taxa with plesiomorphic flight apparatus are also likely to exhibit plesiotypic flight kinematics, then in general the flight of Odonata shows a development from a uniform wing beat pattern to one with much more variation in derived Odonata. Particularly the Libellulidae or Calopterygidae (Bybee et al., 2008; Carle et al., 2008; Dumont et al., 2005, 2010) show much more variation (Rüppell, 1989). Hence the morphological prerequisites of different systematic groups result in part from their phylogenetic development but also from the structural and aerodynamic requirements of their characteristic flight-dependent behaviour, which leads to different flight patterns.

However, insect wings may have functions in addition to flying: they can be important for thermoregulation (Heinrich, 1986, 1993; Kingsolver & Koehl, 1985; Outomuro & Ocharan, 2011; Tsubaki et al., 2010) and for communication (Corbet, 2004; Schultz & Fincke, 2009). While in many odonate species the bodies of males are colourful, as seen by the human eye, the wings are in most cases clear. In some families, such as the Euphaeidae, Polythoridae, Pseudolestidae, Thaumtoneuridae, Calopterygidae, Pseudostigmatidae, a few Aeshnidae, some Chlorogomphidae and many Libellulidae, the males have often conspicuously coloured wings (Silsby, 2001), and the males of many of these species display their wings in courtship behaviour (reviewed by Fincke, 1997). Male calopterygid damselflies usually possess coloured wings (Hooper et al., 1999) that have been interpreted as a signal trait (Córdoba-Aguilar & Cordero Rivera, 2005; Siva-Jothy, 1999). The colouration of the wings in species of Calopterygidae has been tied to fitness-related characters such as fat deposits and social status (Fitzstephens & Getty, 2000; Plais-tow & Siva-Jothy, 1996; Siva-Jothy, 1999, 2000). The size and quality of these ornaments lead to reproductive advantages by increasing territorial and mating success (Contreras-Garduño et al., 2006, 2008; Grether, 1996a, 1996b; Hilfert-Rüppell, 2004; Rantala et al., 2000; Siva-Jothy, 1999). These investigations focused on the structural characters of the coloured wings and on their behavioural and evolutionary consequences but not on the flight of the males in which the ornaments are displayed. Competing males of Odonata are most often flying when they meet at reproduction sites. Each special flight pattern appears as a conspicuous optical stimulus to which the contestant reacts by its own flight pattern (Córdoba-Aguilar & Cordero Rivera, 2005). Until now these flights have only been studied in Calopterygidae and Pseudostigmatidae, which fly relative slowly (Pajunen, 1966; Rüppell, 1985; Rüppell & Fincke, 1989). These species show a special flight by flapping their wings in parallel (i.e. in phase). Furthermore *C. splendens* exhibits a variety of different flight patterns: including elaborate manoeuvres, high velocity flight, wing pauses, and gliding with half-spread wings (Rüppell & Hilfert-Rüppell, 2009b). Males of *Megaloprepus caerulatus* do not exhibit as many different flight styles. Mostly they hover in front of another male, displaying their wings beating simultaneously in parallel (Rüppell & Fincke, 1989). This kind of flight occurs only in the presence of an adversary, and so very probably has a signalling function (e.g. Schultz & Fincke, 2009).

The flight performance of male Anisoptera with coloured wings is, to date, unknown because of difficulties in collecting data from their very fast and erratic flight. Hints from our own unpublished observations of libellulids with coloured wings (*Rhyothemis fuliginosa* (G. Rüppell,

unpublished observation on *Ryothemis fuliginosa*, Nakamura, Japan, 1993) and *Neurothemis* sp. (G. Rüppell, unpublished observation on *Neurothemis* spec., Kerala, India, 1989)) and those of others (*Palpopleura lucia* (F. Suhling, unpublished observation on *Palpopleura lucia*, Okavango near Rundu, Namibia, 2006)) suggest that these males also beat their wings in a specific way. New digital filming technology, which provides sufficient resolution and long-lasting recordings, now make it possible to collect data systematically (Rüppell & Hilfert-Rüppell, 2009a). The aim of this study is to find out whether damselflies and dragonflies with clear and with coloured wings fly differently. The analysis had to be restricted to comparable flight manoeuvres so as to exclude motivational and aerodynamic influences as far as possible. We focused on male–male encounters at the reproduction site when competing for territories or females. The motivation for flight must be very similar for both opponents: eject the other male and obtain access to the limited resource (i.e. females). Thus the flight parameters of encountering males with clear wings and with coloured wings were compared.

If coloured wings function as signals to other males, then competing males should exhibit their wings conspicuously. Our main hypothesis was that males with coloured wings (i.e. used in communication) move their wings to display the wing ornaments and hence fly differently to clear-winged males. If this is a general principle it should be true in both Zygoptera and Anisoptera. Therefore we chose the flight of males of different systematic groups from both suborders, including species presumed to be relatively basal (plesiotypic) and others more derived (apotypic). If in both groups wing colouration proved to be related to similar changes in flight, this would be a strong hint of convergent evolution. Sexual selection, rather than systematic relationships or aerodynamic necessities, probably would be responsible for that.

Material and methods

Male encounters at typical densities were analysed from high-speed films for 10 species in six families (Figure 1) to compare their flight parameters (Table 1). For this comparison we chose species from different systematic positions (according to Bybee et al., 2008; Carle et al., 2008; Dumont et al., 2010; Fleck et al., 2008; Pessacq, 2008) to control for phylogenetic effects on flight characteristics. Within Zygoptera, *Lestes viridis* (Lestidae) represented a more basal clade compared with *Coenagrion puella* (Coenagrionidae) although both have clear wings (= SCLW [species with clear wings]). In contrast, *Calopteryx splendens*, *Neurobasis chinensis* (Calopterygidae) and *Megaloprepus caerulatus* (Pseudostigmatidae) all have coloured wings (= SCOW [species with coloured wings]) and represent more derived groups relative to Lestidae. Similarly, the clear-winged *Aeshna cyanea* represents a more basal family (Aeshnidae), whereas the clear-winged *Nesiothemis farinosa* represents the more derived Libellulidae. The other study species, *Libellula quadrimaculata*, *Trithemis arteriosa* and *Neurothemis fluctuans*, are also Libellulidae, but all have coloured wings.

Although we previously filmed *Calopteryx splendens* (1982–1986) and *Lestes viridis* (1985) we re-filmed these species (2008–2012) in order to obtain enough data for comparisons. For the cluster analysis we also looked at films of flights of *C. splendens* when prey-catching. For comparison we looked at male–male encounters in own slow-motion films of *Anax imperator*, *Brachythemis leucosticta*, *Calopteryx haemorrhoidalis*, *Mecistogaster ornata*, *Mnais nawai* and *Sympetrum pedemontanum*. Other slow-motion films of *Megaloprepus caerulatus* from 1985 and 1986 were re-analysed with respect to additional variables. In this species we included only flights of large males, because the wing beat frequencies in general are related to body size (Rüppell, 1989). Males were always filmed under sunny conditions with little or no wind, at temperatures in hot climates between 26 and 32°C (France, Namibia, Panama, Thailand,) and between 22 and 28°C in Germany. Until 2004, we filmed using a 16 mm film slow-motion camera LOCAM (model

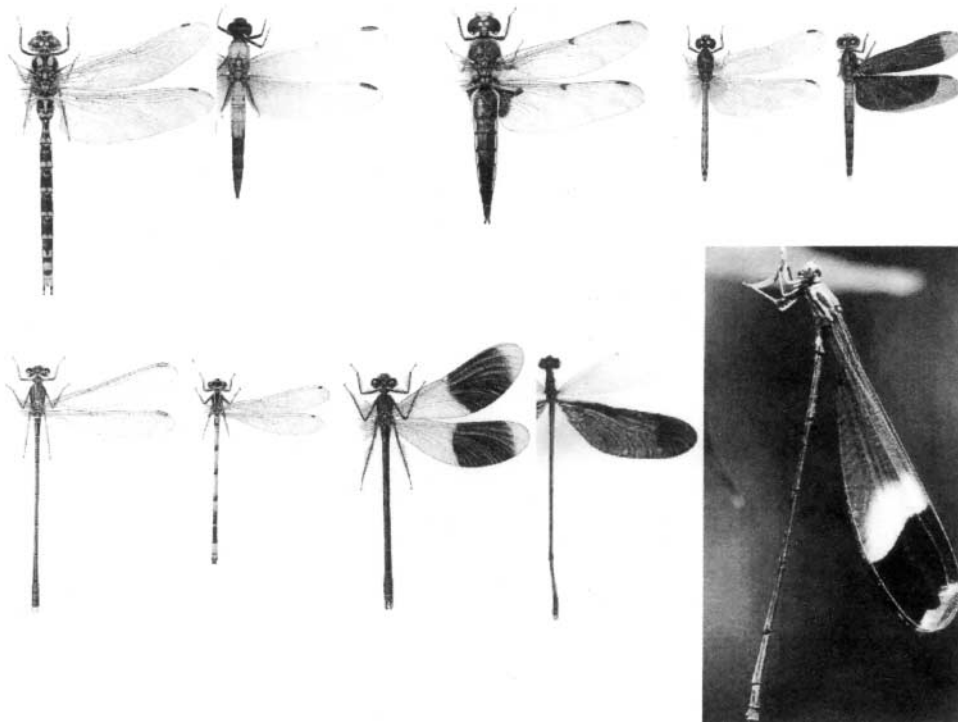


Figure 1. The species investigated: Anisoptera (top – left to right): *Aeshna cyanea*, *Nesciothemis farinosa*, *Libellula quadrimaculata*, *Trithemis arteriosa*, *Neurothemis fluctuans*. Zygoptera (bottom – left to right): *Lestes viridis*, *Coenagrion puella*, *Calopteryx splendens*, *Neurobasis chinensis*, *Megaloprepus caerulatus*. The colours of wings are: *L. quadrimaculata* – wing bases amber and also large blackish triangles at the base of the hind wings; yellowish stripes at the leading edges; *T. arteriosa* – red wing bases and red veins; *N. fluctuans* – dark brown; *C. splendens* – dark blue bands; *N. chinensis* – metallic green hind wings; *M. caerulatus* – all wings have dark blue spots distal to a white band in males. (Figures by J. Craves, R. Lewington, B. A. Orr, B. Strnadova, and W. & M. Tarboton).

51, USA); thereafter we used a digital camera (Casio Pro EX F1, Japan). The filming frequencies were 250–600 f/s. In all cases the camera was pre-focused to the flight area of the dragonflies and moved parallel to the movements of the dragonflies, without looking simultaneously through the viewfinder and only briefly at the digital camera screen.

To characterize the species studied we used the body length measurements reported by Fincke (1992), Tarboton and Tarboton (2002), Dijkstra (2006), Suhling & Martens (2007) and Günther (personal communication, 2012). We measured males of *Neurothemis fluctuans* in the field by photographing them with a reference scale on graph paper. We measured the body lengths and wing areas using the software ImageJ (National Institutes of Health, Bethesda, Maryland, USA).

To analyse the 16 mm films we used a single frame projector (NAC Image Technology, Japan, model DF16B) and the QuickTime programme (Version 7.55.90.70) for the digital images. To obtain the wing beat frequencies we counted the frames of the film, if possible separated into downstroke, upstroke and wing beat pauses. To reduce the possibility of errors we sometimes used the means of 2–4 measures. To obtain the wing beat frequency the exposure rate was divided by the numbers of frames per wing beat. For the 16 mm films we used time marks on the film at an interval of 1/100 s; for the digital images we checked the written exposure time using a stopwatch. Flight velocities were measured by marking the shift of an individual's image on a movable foil placed on the computer screen. When the camera was moved, prominent structures in the background were drawn on the foil and were covered by these structures on the film when measuring the dragonfly's body displacement. Wing beat angles (i.e. the angle through which the

Table 1. Species and locations of Odonata investigated; body lengths (in *M. caerulatus*, wing lengths); total numbers of flights and wing beats filmed; whether colours occur in either wing and if so whether only in the hind wings (hw) or in both pairs of wings (fw hw); wing beat frequencies during male–male encounters; and duration of wing pauses as a percentage of the whole flight duration during encounters.

Taxon	Body length (mm)	Coloured wings	Number of flights	Number of wing beats	Wing beat frequency (Hz; mean \pm S.D)	Pauses as % of total flight time	Place and time filmed
ZYGOPTERA							
Lestidae							
<i>Lestes viridis</i>	39–48	No	8	69	45 \pm 3.7	0	Germany 52°26' N, 10°23' E, 1985, 2012
Coenagrionidae							
<i>Coenagrion puella</i>	33–35	No	11	183	38 \pm 5.2	0	Germany 2009–2011
Calopterygidae							
<i>Calopteryx splendens</i>	45–48	fw hw	6	234	17.3 \pm 6.6	25.7	Germany 2008–2011
<i>Neurobasis chinensis</i>	56–62	hw	7	74	20.2 \pm 6.8	32.4	Thailand 8°37' N, 98°14' E, 2009
Pseudostigmatidae							
<i>Megaloprepus caerulatus</i>	58.6–73.4*	fw hw	8	58	11.2 \pm 4.2	54.7**	Panama 9°9' N, 79°51' E, 1986
ANISOPTERA							
Aeshnidae							
<i>Aeshna cyanea</i>	67–76	No	7	160	42.9 \pm 5.3	0	Germany 2008–2011
Libellulidae							
<i>Nesiothemis farinosa</i>	40–45	No	5	198	57.3 \pm 9.3	0	Namibia 22°34' S, 17°5' E, 2004
<i>Libellula quadrimaculata</i>	40–48	fw hw	5	93	36.4 \pm 8.6	24.3	Germany 2011
<i>Trithemis arteriosa</i>	31–38	fw hw	2	42	46.3 \pm 17.6	55.7	Namibia 2004
<i>Neurothemis fluctuans</i>	27.4–35.4	fw hw	6	119	40.8 \pm 15.4	fw 46.8 hw 32.7	Thailand 2009

*Wing length.

**During descending flight only.

wing beats) were calculated only when the movement of the dragonflies and the camera's filming direction were at a right angle with respect to each other.

To test for differences in the wing beat frequencies among all species we used univariate analyses of variance. To compare the mean values of the wing beat frequencies between the groups we used the Mann–Whitney U-test, because most of the data are far from a normal distribution. We hypothesized that particularly variance in wing beat frequency between the groups (SCOW and SCLW) may be inhomogenous. We used a Levene test to evaluate this independently for both suborders (Zygoptera and Anisoptera).

To identify taxa with similar flight patterns we used a cluster analysis (Euclidean distances). We chose six characters for the latter: the mean, standard deviation, and range of wing beat frequency, the ratio of summed duration of wing beat pauses to duration of flight, and the range of variation of the phase relationships of the fore and hind wings and of the stroke angle (both based on ranking the characteristics of the 10 species).

Results

Wing beat frequencies

The wing beat frequencies (number of wing beats per second = Hz) during male–male encounters differed among species (ANOVA, $p < 0.01$). In general, wing beat frequencies were clearly lower in Zygoptera than in Anisoptera (Figures 2 and 3), and this applied particularly to zygopterans with coloured wings, with *M. caerulatus* having the lowest frequency of all. In Anisoptera the frequency ranges were much greater in SCOW than in SCLW (Figures 2 and 3), with extreme values (small black circles) only being present in SCOW. Comparisons of the lowest and highest wing beat

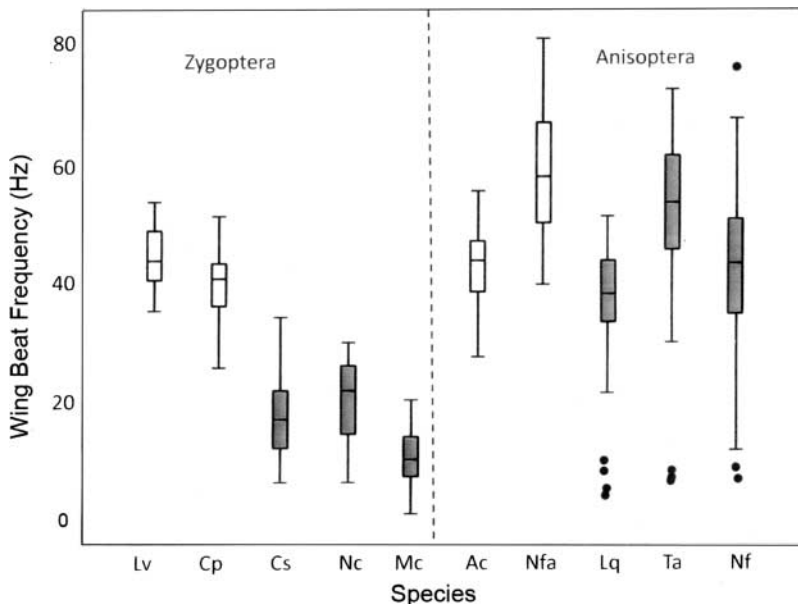


Figure 2. Wing beat frequencies (Hz) of odonate males at encounters. Bars include 50% of each data set, horizontal lines in the bars show the median, the vertical lines with small terminal crossbars show the range excluding outliers, and the small filled circles are outliers. Zygoptera with clear wings: Lv – *Lestes viridis*, Cp – *Coenagrion puella*; Zygoptera with coloured wings (vertically hatched bars): Cs – *Calopteryx splendens*, Nc – *Neurobasis chinensis*, Mc – *Megaloprepus caerulatus*; Anisoptera with clear wings: Ac – *Aeshna cyanea*, Nfa – *Nesciothemis farinosa*; Anisoptera with coloured wings (vertically hatched bars): Lq – *Libellula quadrimaculata*, Ta – *Trithemis arteriosa*, Nf – *Neurothemis fluctuans*.

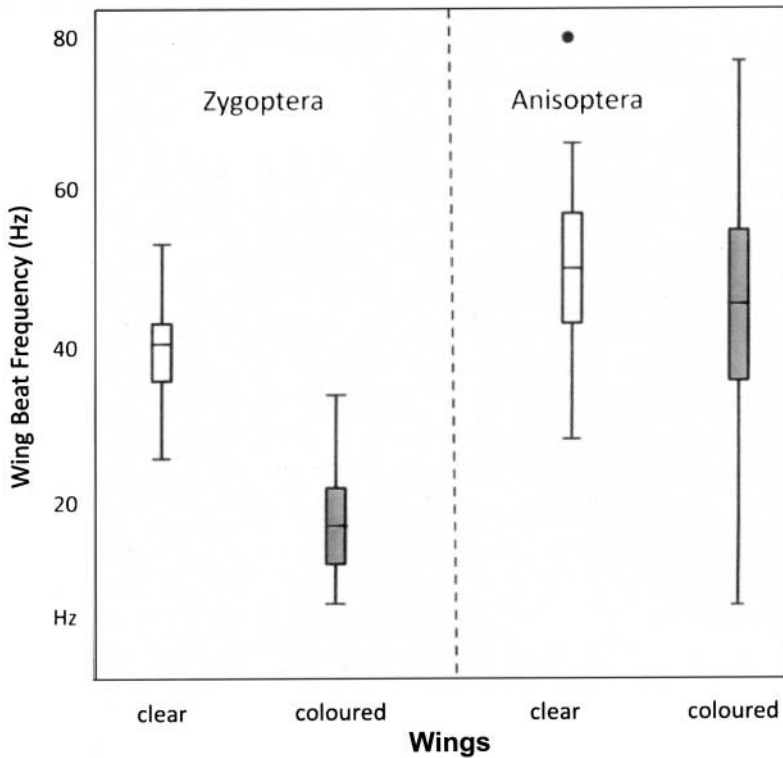


Figure 3. Comparison of the wing beat frequencies between Zygoptera and Anisoptera with clear and coloured wings (graph symbols as in Figure 2).

frequencies showed that all species with coloured wings, when encountering other males, had a very wide range with especially low values (Figure 2). In Anisoptera the relatively small species, *N. fluctuans*, with large wing ornaments, had no higher median wing beat frequencies than the larger *A. cyanea* (Mann–Whitney U, $p = 0.411$). That of *L. quadrimaculata*, of median size (Table 1) with only small ornaments, by contrast differed from the frequencies of *A. cyanea* significantly ($p < 0.01$).

We then compared all SCLW with all SCOW of both suborders. The wing beat frequencies of the two groups within each suborder differed significantly (U-test, both $p < 0.01$) (Figure 3). The homogeneity of variance of the mean wing beat frequencies also differed between SCOW and in SCLW in both suborders (Levene test, for both comparisons, $p < 0.01$). It was always lower in SCOW. To discriminate the variations of the wing beat frequencies we calculated the standard deviation as a percentage of the mean beat frequency (= coefficient of variation, CV) and found large differences (Figure 4). In SCOW the CV was 3–4 times higher than in SCLW. However, males of *L. quadrimaculata*, which possess only small coloured areas on the wings, had less variable wing beat frequencies, as shown by the relatively low values of the standard deviation (Table 1) and the CV (Figure 4).

Kinematics

Phase relationships between fore and hind wings

At male–male encounters the two pairs of wings were beaten in different patterns: Zygoptera SCLW (*L. viridis* and *C. puella*) showed counter stroking or only a slight phase shift, the forewings

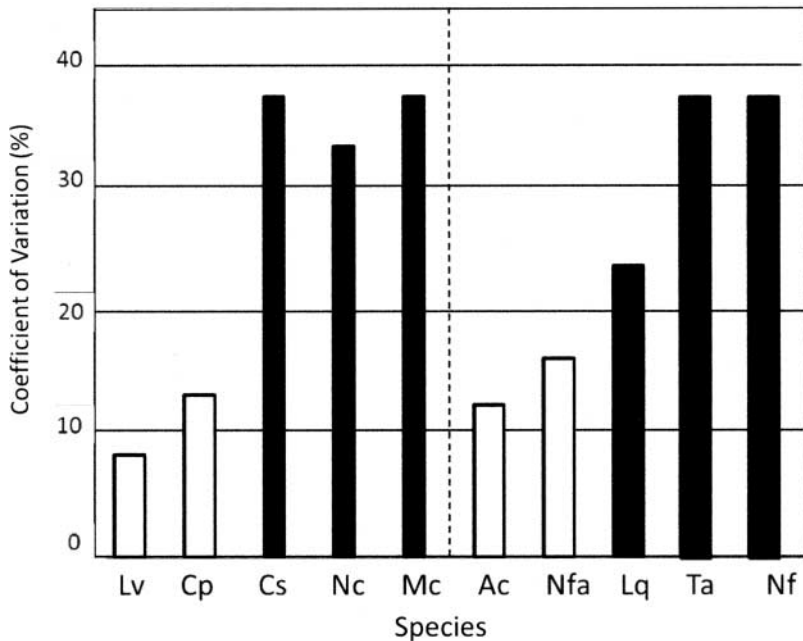


Figure 4. Coefficient of variation (= standard deviation as a percentage of the mean wing beat frequencies) of the wing beat frequencies during male–male encounters. Light bars = species with clear wings (SCLW), dark bars = species with coloured wings (SCOW), Species abbreviations as in Figure 2).

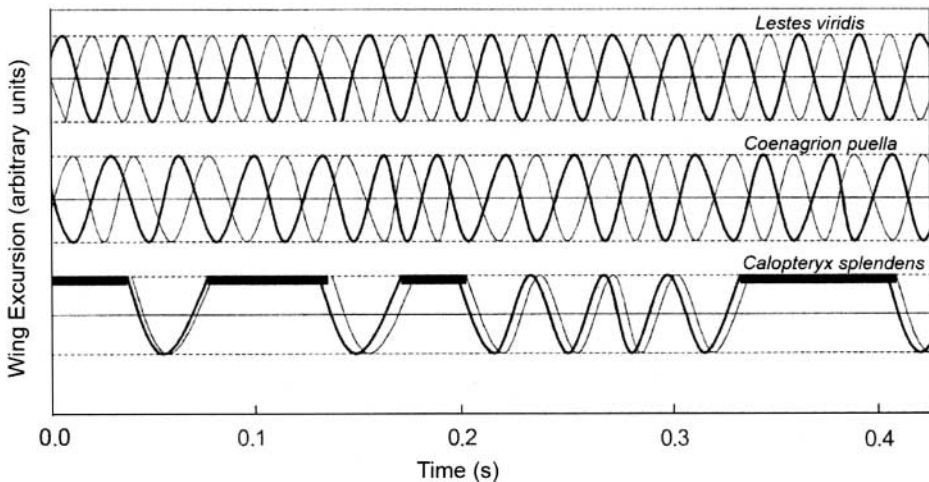


Figure 5. Wing beat patterns of encountering males of Zygoptera (semi-schematic). Top: *Lestes viridis* counterstroking; middle: *Coenagrion puella* counter stroking and sometimes phase shifting; bottom: *Calopteryx splendens* parallel stroking with pauses with the folded wings in the backward position (horizontal black bars). Dark lines illustrate the displacements of fore wings, light lines of hind wings. Lines going down, down stroke; lines going up, upstroke. X-axis = seconds.

leading the wing movement. In contrast the SCOW (*C. splendens* and *M. caerulatus*) beat their fore and hind wings nearly parallel (i.e. in phase), the hind wings having a delay of only 5–10% of the whole wing beat duration during the upstroke in *C. splendens* (Figure 5).

In all Anisoptera we found a phase-shifted wing beating of the fore and hind wings, the hind wings leading and the forewings following by about a quarter of a whole wing beat period.

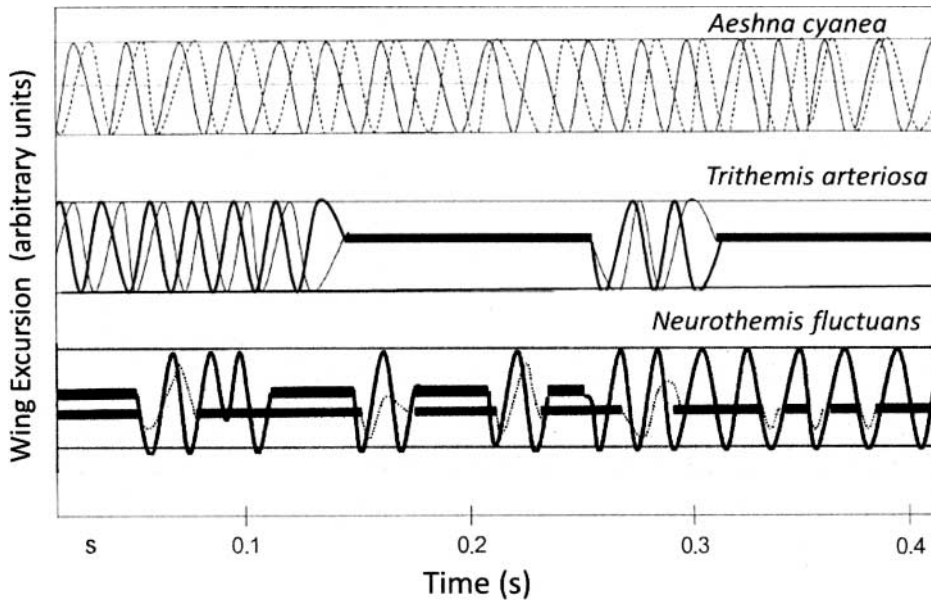


Figure 6. Wing beat patterns of encountering males of Anisoptera (semi-schematic). Top: *Aeshna cyanea* (unbroken lines, displacements of hind wings; broken lines, of fore wings); middle *Trithemis arteriosa* (thick lines, displacements of hind wings; thin lines, of fore wings); bottom: *Neurothemis fluctuans* (unbroken lines, displacement of hind wings; broken lines, of fore wings). Lines going down, down stroke; lines going up, upstroke. X-axis = seconds. Horizontal black bars, pauses with wings spread. Note the small wing beat angles (= small amplitudes) of the fore wings in *N. fluctuans*.

However, this pattern was not steady, as the example of *A. cyanea* shows (Figure 6). In fights of *A. cyanea* and *L. quadrimaculata*, short counter stroking could be seen when hovering or climbing. One or two parallel wing beats of fore and hind wings occurred in fights when flying fast backwards. *Neurothemis fluctuans* (SCOW), however, varied these phase relationships widely (Figure 6).

Beating pauses and wing beat angle in flight

Pauses of both wings (i.e. interruption of wing beats) occurred frequently in male encounters in SCOW. Pauses were least frequent in *L. quadrimaculata* and often much more frequent in *T. arteriosa* and *M. caerulatus*. The value for the latter species was the result from a descending flight. In level or climbing flights, no wing pauses were observed in *M. caerulatus* (seven flights). Also the wing pauses in *L. quadrimaculata* were mostly exhibited in brief downward or forward flights. The high values of wing pauses as a percentage of whole flight duration (55.7%) in *Trithemis arteriosa* were a result of measurements made in the morning, when territories were first established. Later in the day, when the territorial male circled around the intruder at high velocities (7.6; 8.9 and 3.9 m s^{-1}), we found lower values (24.3%, $n = 88$ wing beats). In *C. splendens* wing beat pauses were shorter when males flew fast. Thus, in fast pursuing flight (max 3.75 m s^{-1}) the cumulative percentage of time during pauses was only 17% ($n = 27$ wing beats) while at relatively slow undulating flight (around 0.6 m s^{-1}) it was 56% ($n = 118$ wing beats).

Wing pauses of only one pair of wings were seen in *C. splendens*, *N. chinensis*, *T. arteriosa* and *N. fluctuans*. In *C. splendens* the forewings stopped beating during passages of lateral threatening flight, which often occurred during horizontal zigzag (undulating) flight, in *T. arteriosa* after periods of gliding, and in *N. fluctuans* during frontal encounters. Furthermore, the males of the last species reduced the beating angles of the forewings from about 70° to 90° to $5\text{--}10^\circ$ to 40°

when approaching a perched conspecific male, while the hind wings beat normally. During some pursuing flights of *N. chinensis* the hind wings of both males (with a metallic shining surface) stopped beating, being held nearly motionless, with the leading male flying in a laterally undulating path. When performing a banked turn towards the middle of the flight paths, only the lower of the hind wings was stroking, and only at very small angles. This was also the case when circling around each other for some seconds. Only the clear forewings were beating at the maximum angle.

During frontal encounters, males of SCOW sometimes reduced the beating angles of both pairs of wings at the end of the down stroke and beat them mostly in the frontal range of normal wing beat angles. In males of *C. splendens* the maximum wing beat angle of 90–110°, with wing-clapping at the end of the upstroke, was reduced to only 40–70° without wing-clapping. *Megaloprepus caerulatus* in a descending flight beat its wings at an angle of 10–30° in contrast to 100–130° in all other flights.

Grouping of species

By combining wing beat frequencies with five other flight characters (see Material and methods) we obtained a clear division into two clusters representing SCLW and SCOW (Figure 7). The only exception was *C. splendens* flying toward prey and back to the perch. We included those films in this study to compare “normal” flight with the flight of encountering males. These prey flights clustered within the SCLW, but the males of *C. splendens* threatening each other at encounters grouped among all the other males of species with wing ornaments.

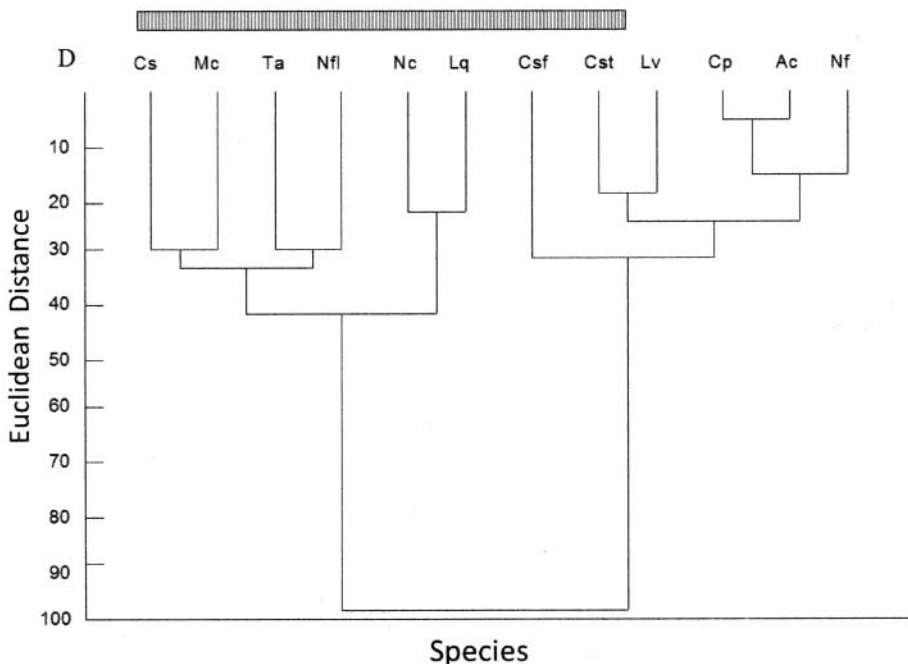


Figure 7. Similarities of flight characteristics at male encounters. All species with coloured wings (SCOW, vertically hatched bar) cluster together (left), as did the species with clear wings (SCLW) (right). However, *C. splendens* flying towards prey (Cst) is within the SCLW; still within it but a little further separated is *C. splendens* flying away from prey to the perch (Csf). (Cluster analysis explains 84% of the variability).

Special behaviour during encounters

In both Zygoptera and Anisoptera, all males of investigated SCLW, with the exception of *N. farinosa*, fought with physical contact when meeting at the reproduction site, pursuing and ramming the rival or striking it with the legs (Zygoptera) or legs and head (Anisoptera). These attacks were often very intense and occurred at high flight velocities, leading to crashes in the Aeshnidae (*A. cyanea*, *Anax imperator*). *N. farinosa* males hovered in front of each other or circled around the rival in narrow flight curves, until one male flew away. Physical attacks were not seen in this species.

Males of SCOW did not make contact with each other during encounters (at normal densities). The general flight styles, as described in the introduction, of *C. splendens* during male–male encounters were similar in the other *Calopteryx* species, *C. virgo* and *C. haemorrhoidalis*. However, we saw differences in the use of the flight space. The last two species varied their flight paths more in a vertical direction, more often showing vertical undulating flight. *M. nawaii* sometimes ascended in a circling flight of up to 10 m, then immediately dived back to the ground. All the last three calopterygids occur in narrow running waters, whereas *C. splendens* also occurs in wider rivers (Rüppell et al., 2005).

Competing males of *T. arteriosa* also circled around their adversaries, as in *Nesciothemis farinosa*. Males of *N. fluctuans*, however, erected the long axis of their bodies as much as 80° to the horizontal and flew in this upright position in front of each other. Furthermore, the males often beat only the hind wings, while the outspread fore wings were presented to the rival and were motionless most of the time or were moved only at low wing beat angles (see above). Losing height by this reduced wing beating was compensated by bursts of normal wing beats. This sometimes resulted in an undulating flight path, similar to such flight passages of Calopterygidae (filmed in *C. splendens*, *C. virgo*, *C. haemorrhoidalis* and *N. chinensis*). These threatening flights in *N. fluctuans* ended an encounter if the contestants differed obviously in size and the smaller male left ($n = 8$). If threatening with the erected body had no effect, the attacking male often changed to a horizontal body position and headed for the other male with increased speed and wing-beat frequency (up to 55 Hz in contrast to about 35 Hz in other threatening flights) in counter-stroke mode. They also sometimes flew upwards in circling flight, then dived downward, much as described for *M. nawaii*. Nearly all of these attacks chased the rival away.

Discussion

The wing beat frequencies of Odonata are size dependent (Rüppell, 1989). Smaller species in general have higher frequencies than large species. But the differences in the frequencies found here cannot be explained only by this size dependence. In Anisoptera the smaller species *N. fluctuans* with coloured wings has similar mean beating frequencies as the much larger *A. cyanea* with clear wings. In Zygoptera the very low frequencies of SCOW in contrast to that of SCLW may be caused partly by the wing pauses. During aggressive encounters of conspecific males at reproduction sites, such flight parameters as wing pauses, variation in wing beat frequencies, and plasticity of phase relationships of fore and hind wings, as well as the variation of flight paths clearly differed between SCOW and SCLW males. This result was the same in both Zygoptera and Anisoptera. The dimensions and the shapes of the bodies and the wings of the species of the two suborders differ markedly (Figure 1). As a result biomechanical factors such as lift production, stiffness, flexibility or resilience of the wings also differ in the two suborders. As in both suborders the SCOW show similar flight variations, e.g. parallel beating of both wing pairs, flying with only one pair of wings, wing beat pauses of all four wings much longer than in SCLW, and special

conspicuous flight paths, this is a strong hint that the wing ornaments and not biomechanical factors cause variation in these flights.

Also, phylogenetic relationships seem to play a limited role in these flight variations. All the different flight parameters lead to clear groupings in cluster analysis, in which SCLW and SCOW are distributed in two separate clusters. *Calopteryx splendens* males flying to or from the prey matched the SCLW. This shows that, within a single species, in SCOW the flight of males changes in the presence of other males. This was also true in *N. fluctuans* and in *T. arteriosa*. Because the results are consistent in both phylogenetic lines, we conclude that functional adaptations rather than systematic relationships led to the flight differences in SCOW and SCLW.

Flight specialization for better recognition of the ornaments?

In Zygoptera SCLW showed a relative steady wing beating pattern, especially the counter stroking Lestidae. In the Coenagrionidae counter stroking also occurred but with a slight phase-shifting between fore and hind wings. In contrast, the males of Calopterygidae (SCOW) and of *M. caerulatus* beat both pairs of wings in parallel, which doubles the visible area of the ornaments from a frontal view. This leads to an optimal presentation of the ornaments. When wings are moved very fast (at wing beat frequencies of about 30–40 Hz) the velocity of the wing tip can reach more than 300 cm s^{-1} (Rüppell, 1989), complicating the perception of details. Many males of SCOW display their wings by holding them still for a short while, either at the end of an upstroke (*Calopteryx* species, Rüppell, 1985, 1989) or midway through a stroke (*T. arteriosa*, *N. fluctuans*). The wing pauses may allow males to evaluate each other's ornament qualities (Contreras-Garduño et al., 2008; Grether, 1996a, 1996b; Hilfert-Rüppell, 2004; Siva-Jothy, 1999). This assumption is supported by the behaviour of *N. chinensis*. The males, with very conspicuous ornaments only on the hind wings, sometimes hold only these hind wings still when flying together with other males. They also do this when a female appears at the oviposition site (Günther, 2006; Orr & Hämäläinen, 2007).

During wing beat pauses the damselflies lose height and velocity, which have to be compensated for by accelerating. Therefore, the parallel beating of both wing pairs is used to supply considerable force (Wang & Russell, 2007). Another increase in force production comes from the clap and fling mechanism, the clapping of the wings all together at the end of the upstroke, increasing lift production considerably (Wakeling & Ellington, 1997). The distance covered during one wing beat in *C. splendens* using clap and fling is three times as great as in *L. viridis* (Zygoptera) although the latter is only a slightly smaller species (Rüppell, 1989). *Megaloprepus caerulatus* also flies using parallel wing beating but normally does not clap the wings together at the end of the upstrokes. However, males can do it and thus are also able to take advantage of the clap and fling mechanism, as a new film analysis shows.

Communicative and aerodynamic needs

As seen above, communicative and aerodynamic requirements may conflict in coloured-wing species. We thus expect a trade-off between these needs in SCOW. Two examples illustrate this. (a) In *M. caerulatus* wing pauses occurred in downward flights, when less lift is needed, rather than in upward or level flights. This restriction may perhaps result from the large size of these giant damselflies. In the much smaller *Calopteryx* species wing pauses are frequent in horizontal or even in short upward flight, too. (b) Several times we filmed males of *C. splendens* intruding into a rival's territory only beating their hind wings. Apparently in response to unintentional height loss, the males added a third wing to provide extra lift and hence flew using three wings stabilizing height loss. The fourth wing was held motionless and directed towards the rival (G. Rüppell,

unpublished observation, Braunschweig, Germany, 2008 and Rüppell, 1985). In contrast, when the aerodynamic needs were lower, signalling was enhanced by displaying as much coloured wing area as possible.

Wing pauses in Calopterygidae may not only serve for communication but may offer short rest periods as well. When approaching a prey the males flew with very high wing beat frequencies and without wing pauses (Table 1); when returning to the perch wing pauses were more frequent.

Signalling flights in Anisoptera

Flight in the Anisoptera has not developed in the same way as in the Zygoptera due to their morphological prerequisites that result in a smaller maximum wing stroke angle and greater restrictions on wing twisting (Pfau, 1986). However, in view of the findings in coloured-winged Zygoptera it is not surprising that Anisoptera males with coloured wings also exhibit special flight patterns when competing in flight, although they are less specialized than the Zygoptera. Anisoptera normally fly by phase-shifting in both pairs of wings (Usherwood & Lehmann, 2008; Wang & Russell, 2007). However, in male Anisoptera with coloured wings this is varied to different degrees during encounters with other males. A slight variation in flight is seen in males of *L. quadrimaculata*, which sometimes glided close to a rival, possibly displaying the coloured wings ($n = 5$). However, much more often the males attacked each other physically ($n = 30$). The short gliding periods at male encounters are not clearly understood. Whether or not this behaviour already has a communication function, it may indicate the initial development of signalling flight behaviour. The similar wing beat frequencies at encounters of the smaller *L. quadrimaculata* in comparison with the larger *A. cyanea* (Figure 2) and the grouping of this species in the group of SCOW (Figure 7) may give evidence for that.

Without any doubt a communication function is established in males of *T. arteriosa* and *N. fluctuans*. They, too, exhibit flight manoeuvres displaying the ornaments only in the presence of other males. Males of *T. arteriosa* often banked toward the other male. Males of *N. fluctuans* showed an exceptional flight variation – erecting the body in front of each other. Seen from the point of view of flight economy this is a handicap. But only by erecting in this way can the entire wing surface be presented to the rival, due to the limited degrees of freedom of the wing joints of Anisoptera which allow mainly forward-downward movements of the wings (Pfau, 1986; Rüppell, 1989). So in males of Anisoptera we found differences of flight in the Libellulidae, ranging from small variations in *L. quadrimaculata*, which possess only small ornaments, through *T. arteriosa* to the well-advanced variations in *N. fluctuans*, which has the largest ornaments. Not only are sizes of the coloured wings different in these three species of Libellulidae but also the elaborateness of the flight and thus the energy expenditure. Gliding with banking probably does not cost as much energy as hovering with an upright posture, sometimes with pauses of the forewings. To find out whether flight behaviour and energy expenditure are in general closely and continuously correlated with wing colouration, it will be necessary to investigate many more species exhibiting incremental differences in wing ornamentation.

Benefits of signalling flight

What could be the benefits of this costly behaviour (Marden & Rollins, 1994; Marden & Waage, 1990; Plaistow & Siva-Jothy, 1996)? It may lower the risk of damage by avoiding fights with physical contact, in contrast to males with clear wings that often collide and ram each other (Campanella & Wolf, 1974; Corbet, 2004; Kaiser, 1985; Wildermuth, 2008), but this seems inadequate by itself to account for the elaborate, species-specific ornaments and energy-costly flights.

Another major cause for the development of the signalling flights could have been optimizing sexual selection. Coloured wings in Calopterygidae have evolved in response to sexual selection (Córdoba-Aguilar, 2002; Córdoba-Aguilar et al., 2007; Serrano-Meneses et al., 2008). If sexual selection was the driving force in the development of coloured wings, signalling flight must have been developed by the same mechanism. The ornaments can be fully presented only in flight. Zygoptera normally fold their wings during perching and in lateral or frontal view the wings of perched Anisoptera are visible only as small lines.

The flight patterns involving parallel wing beating (Wang & Russell, 2007), wing pauses followed by flight accelerations and, in some species, wide flight paths all have a high energy cost and therefore should confer high selective benefit. These flight displays should give accurate information about the quality of the performers and might facilitate the decision of opposing males whether or not to invest in contests. The competition of the males could be a mechanism of intrasexual selection (Grether, 1996b). This needs to be tested by comparing the signalling flight performance of males that differ in their success in encounters. The decision of the females to stay or not might also be influenced by these signalling flights. However, in the species we have studied, males of SCOW have a special courting flight to persuade females to mate with them, as in the Calopterygidae (Rüppell, 1985) and *N. fluctuans* (D. Hilfert-Rüppell, unpublished observation, Kao Lak, Thailand, 2009). This is not known to occur in SCLW.

There is still much more to be learned about the functions and benefits of wing colouration in odonates. Nothing is yet known of wing movements or their significance in females with coloured wings. At high densities, male *C. splendens* may behave as SCLW do by fighting without any signalling flights but with intense physical contact (Hilfert-Rüppell & Rüppell, 2008). In some species, coloured wings may function for concealment or misdirection as well. Thus slow-motion films of *Mecistogaster ornata*, *Brachythemis leucosticta* and *Sympetrum pedemontanum* lead to the plausible speculation that their small coloured wing spots positioned more distally may serve for camouflage. All three of these species at male encounters flew by counter stroking or phase shifted wing beats, without considerable wing pauses. Their flight patterns meant that the shape of the owner is camouflaged by the flickering dark ornaments in the two libellulid species or, in the case of *M. ornata*, they may resemble small insects.

Coloured wings do affect the flight of odonates. But we are not able yet to quantify the full effects, because the dragonfly visual spectrum is different to that of humans. Whether other effects of the wings, such as UV reflections, as in *M. caerulatus* (Hilton, 1986; Schultz & Fincke, 2009), or the age-dependent effects of the wax coverage of body and wings (Kuitunen & Gorb, 2011), play a role in communication remains to be proved in each case.

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